



Altered aluminum inhibition of soybean root elongation in the presence of magnesium

Ivo R. Silva¹, T. Jot Smyth^{1,4}, Daniel W. Israel² & Thomas W. Rufty³

¹Department of Soil Science, ²Department of Soil Science and USDA-ARS, and ³Department of Crop Science, North Carolina State University, Raleigh, NC, 27695-7619, USA. ⁴Corresponding author*

Received 20 June 2000. Accepted in revised form 20 November 2000

Key words: aluminum tolerance, calcium, cation amelioration, magnesium, soybean, wheat

Abstract

Variations in genotype rankings among screenings for Al tolerance in hydroponics may be related to differences in the composition of the solutions. In the present study, we investigated the involvement of Mg ions in modifying Al rhizotoxicity in soybeans. Root elongation was strongly inhibited by Al in a simple, 800 μM CaSO_4 solution, but elongation increased noticeably when the solutions also contained Mg. Amelioration of Al rhizotoxicity was not associated with an increase in ionic strength of treatment solutions because Al^{3+} activities were kept constant. Concentration series experiments indicated that the Mg effect occurred in the μM range, while Ca amelioration of Al toxicity occurred at mM concentrations. The positive effect of Mg on root elongation was greatest for Al-sensitive genotypes and minimized genotypic differences for Al-tolerance. The Mg protection against Al rhizotoxicity apparently does not occur with all species, because it was not observed in Atlas and Scout 66 wheat varieties. The ability of Mg to ameliorate Al toxicity in soybean at μM levels suggests the involvement of distinct physiological factors.

Introduction

Aluminum toxicity is a major constraint to crop productivity in acid soils (Kochian, 1995). Although liming minimizes Al toxicity, this amendment often is not readily available or is very expensive (Sanchez and Salinas, 1981). When lime is added, effects generally are confined to surface soil layers, with little impact on acidity and Al toxicity in the subsoil. Thus, acid conditions and Al toxicity can persist in subsoils, limiting deep root penetration and predisposing crops to drought (Carter and Rufty, 1993; Goldman et al., 1989; Ritchey et al., 1983). An alternative to such management problems is the identification and development of Al-tolerant cultivars (Barceló et al., 1996).

Screening for Al tolerance with field trials requires access to land with relatively uniform acid soils. Few field sites in industrialized countries, where much of

the research is done, meet the minimum experimental requirements (Campbell and Carter, 1990). Other adverse soil factors under acidic conditions, such as Mn^{2+} toxicity and P deficiency, may also confound results. Because of the field limitations, numerous attempts have been made to select germplasm for Al tolerance under hydroponic conditions (Horst and Klotz, 1990; Howeler, 1991; Spehar, 1994; Villagarcia et al., 2000).

Hydroponic screening is not free of difficulties. The pH-dependence of the toxic monovalent Al ions (Kinraide, 1991) requires strict pH control. Chemical interactions of Al with SO_4 and PO_4 can lower the activity of Al^{3+} in solution (Grauer, 1993; Kinraide et al., 1985; Kinraide, 1997; Sanzonowicz et al., 1998). There is also evidence that changes in Ca and Mg concentration, in the mM range, can reduce Al accumulation at the root surface and diminish Al rhizotoxicity (Grauer and Horst, 1992; Kinraide and Parker, 1987; Kinraide, 1994; Ryan et al., 1997). Variable solution compositions most likely have contributed to

* FAX No: 001-(919)515-7422. E-mail: jot_smyth@ncsu.edu

the altered ranking of genotypes for Al-tolerance in experiments using hydroponic culture (Edmeades et al., 1991; Lazof and Holland, 1999; Spehar, 1994; Wheeler and Edmeads, 1995a).

The objective of the present study was to examine the interaction between Mg and Al on root elongation of soybean genotypes in solution culture. The results indicate that μM concentrations of Mg alleviate Al inhibition of root growth and the effects are clearly different from those associated with Ca.

Materials and methods

A number of soybean [*Glycine max* (L.) Merrill] genotypes with varying degrees of Al tolerance were used in a series of experiments. The genotypes were: cvs Essex, Young, Ransom, Biloxi and Flambeau, and the plant introduction 416937 (PI). Wheat [*Triticum aestivum* L.] cvs Atlas and Scout also were used in some experiments. Various Ca and Mg concentrations up to 5.0 mM were tested at Al^{3+} activities varying from 0 to 23 μM , at a constant pH of 4.2. The specific treatments and genotypes used in each experiment are detailed in the 'Results' section.

Soybean and wheat seeds were germinated in paper towels in darkness at 25 °C and 98% relative humidity in a controlled-environment chamber. The germinating seeds were kept moist by capillary action from a 100 μM CaSO_4 solution. After 3 d, seedlings were selected for uniformity of root length and placed into continuous flow hydroponic culture systems. Light was provided by high pressure sodium vapor and metal halide lamps at $850 \pm 50 \mu\text{moles m}^{-2} \text{s}^{-1}$ at the top of the culture tanks. The culture solution temperature was 24 ± 1 °C, and the pH was maintained at 4.2 ± 0.1 with continuous monitoring and automatic additions of 100 mM H_2SO_4 . In all experiments, the basal nutrient solution was 800 μM CaSO_4 . This solution was used in order to provide adequate Ca supply and offset H^+ toxicity (Sansonowicz et al., 1998).

After 24 h of acclimation in the pretreatment basal solution, tap root length of individual seedlings was measured prior to initiation of Al treatments. Tap root lengths were between 12 and 15 cm at this time. Tap root length of individual seedlings was measured again after exposure to treatment solutions for 72 h. Aluminum from an acidified 100 mM AlCl_3 stock solution was added to the basal solution to establish different Al^{3+} activities. In some cases, other nutrients were added to the hydroponic solutions to evaluate

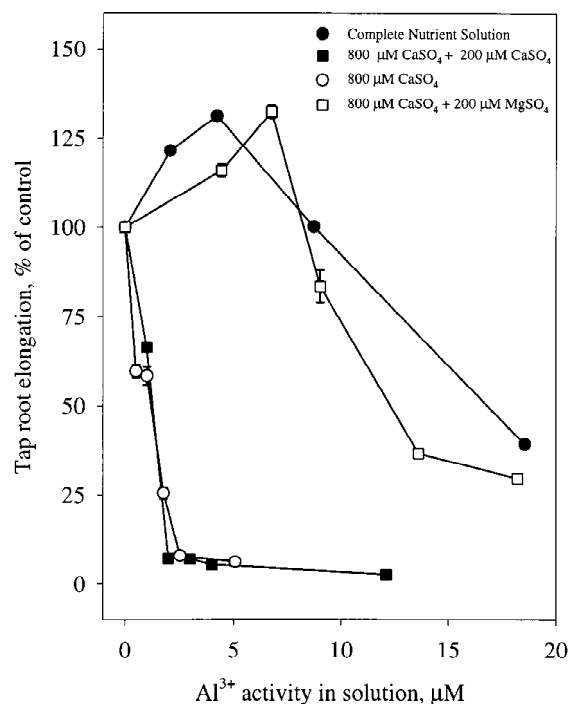


Figure 1. Relative tap root elongation of soybean genotype Essex as a function of nutrient solution composition. Bars denote standard errors.

their effects on the Al^{3+} inhibition of root elongation. The composition of the complete nutrient solution, when used, was (in μM) 300 KNO_3 , 50 KH_2PO_4 , 200 MgSO_4 , 5 FeSO_4 , 800 CaSO_4 , 5.7 H_3BO_3 , 1.1 MnCl_2 , 1.0 ZnSO_4 , 0.12 CuSO_4 and 0.06 Na_2MoO_4 . In all experiments, Al^{3+} activities in solution were estimated using the default set of constants in the GEOCHEM-PC software (Parker et al., 1995).

Root elongation is presented as a % of the control, that is: (root elongation in the presence of Al)/(root elongation in the absence of Al)*100. Each datum point for a treatment represents measurements from approximately 20 individual plants. The experiments were carried out twice and results were pooled.

Results

Nutrient solution effects on Al rhizotoxicity

Initial experiments were conducted with the Al-sensitive soybean cultivar Essex to determine whether response in root elongation to Al changed when the composition of the nutrient solution was altered. Results indeed indicated that was the case. When seed-

lings were exposed to solution with a series of Al^{3+} activities in the presence of only $800 \mu\text{M}$ CaSO_4 , there was a sharp reduction in root elongation, with 50% inhibition occurring between 1 and $2 \mu\text{M}$ Al^{3+} activity (Figure 1). However, when the $800 \mu\text{M}$ CaSO_4 was combined with a complete nutrient solution, root elongation was stimulated in the presence of Al up to $10 \mu\text{M}$ Al^{3+} activity. In the presence of a complete nutrient solution, 50% inhibition of root elongation occurred between 15 and $20 \mu\text{M}$ Al^{3+} activity.

The addition of $200 \mu\text{M}$ Mg to solution with only Al and $800 \mu\text{M}$ CaSO_4 accounted for most of the enhanced root elongation obtained with the complete nutrient solution (Figure 1). Supplementing the $800 \mu\text{M}$ CaSO_4 solution with an additional $200 \mu\text{M}$ CaSO_4 failed to alleviate Al inhibition. Previous investigations have shown that PO_4 can alleviate Al rhizotoxicity for several crop species (Alva et al., 1986; Kinraide et al., 1985). When $50 \mu\text{M}$ P was omitted from the complete nutrient solution in our experiments, root elongation in the presence of Al increased by less than 5%, indicating that our GEOCHEM-based adjustment of solution Al concentrations properly accounted for the formation of non-toxic Al-phosphate complexes in this circumstance.

Magnesium modifies Al-sensitivity of soybean genotypes

The magnitude of Mg alleviation of Al rhizotoxicity in soybean and the associated changes in genotypic rankings can be seen in Figures 2 and 3. In separate experiments, groups of three genotypes with known differences in sensitivity to Al were exposed to a range of Al^{3+} activities in solutions with either $800 \mu\text{M}$ CaSO_4 or a combination of $800 \mu\text{M}$ CaSO_4 and $200 \mu\text{M}$ MgSO_4 . In the first set of experiments, inhibition of root elongation for Al tolerant PI was consistently less than the susceptible cvs. Essex and Young in $800 \mu\text{M}$ CaSO_4 at Al^{3+} activities up to $3 \mu\text{M}$ (Figure 2A). When the same genotypes were exposed to solutions supplemented with Mg, both the inhibition of root elongation and differences among the genotypes decreased (Figure 2B). In a second set of experiments, root elongation of cultivars Biloxi and Flambeau was superior to cv Ransom at Al^{3+} activities up to $2 \mu\text{M}$ in the of $800 \mu\text{M}$ CaSO_4 solution (Figure 3A). The addition of $200 \mu\text{M}$ Mg to the basal solution decreased the inhibition of root elongation by Al for all genotypes and minimized genotypic differences. Root elongation

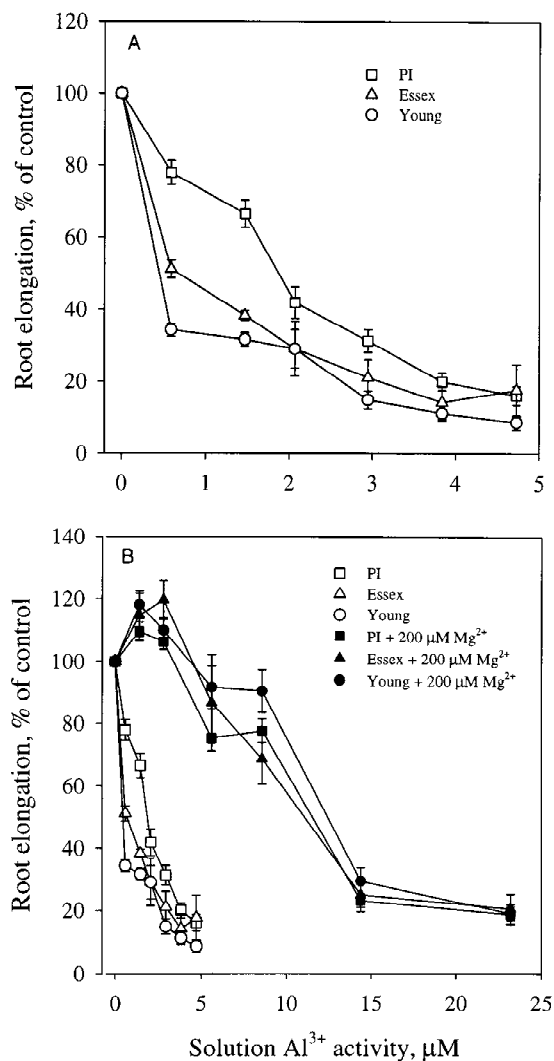


Figure 2. Relative tap root elongation of soybean genotypes PI, Essex and Young in response to increasing Al^{3+} activities in $800 \mu\text{M}$ CaSO_4 solutions, in either the absence or presence of $200 \mu\text{M}$ Mg. Data in 2A are plotted in 2B to provide a frame of reference with the x-axis change. Bars denote standard errors.

of cv Ransom, for example, was inhibited by more than 60% at $0.5 \mu\text{M}$ Al^{3+} activity in $800 \mu\text{M}$ CaSO_4 alone, whereas elongation of cv Flambeau roots were reduced by less than 10%. In the presence of Mg, more than a 20-fold increase in Al^{3+} activity was required to reach the same inhibition of root elongation of both cultivars and there was no difference in their tolerance to Al (Figure 3B).

Magnesium amelioration of Al rhizotoxicity in wheat

Wheat is one of the most intensively studied species

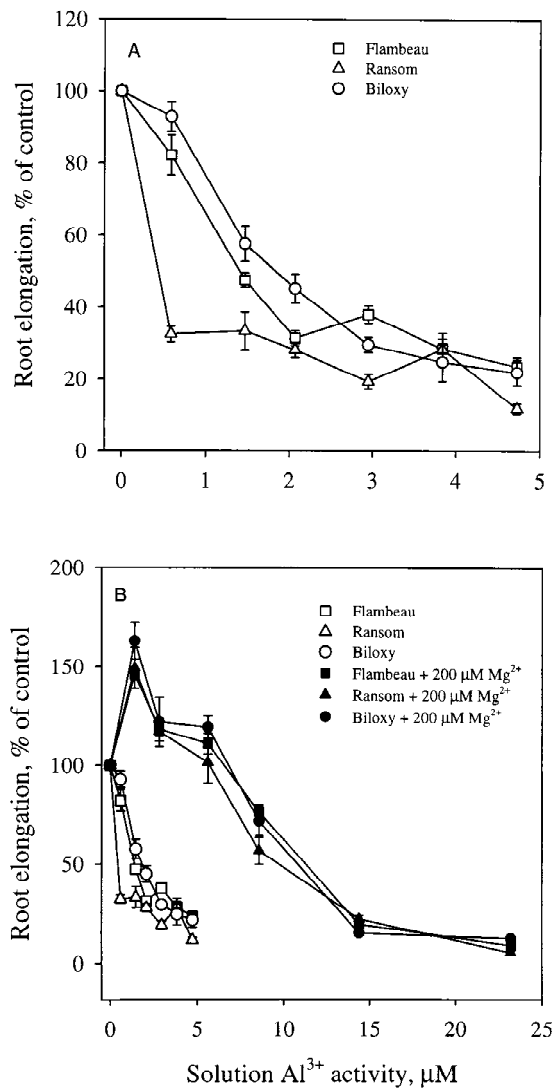


Figure 3. Relative tap root elongation of soybean genotypes Flambeau, Ransom and Bilox in response to increasing Al^{3+} activities in $800 \mu\text{M}$ CaSO_4 solutions, either in the absence or presence of $200 \mu\text{M}$ Mg . Data in 3A are plotted in 3B to provide a frame of reference with the x-axis change. Bars denote standard errors.

in the area of Al toxicity. In the present investigation, experiments were conducted with this species to determine whether the ameliorative effect of Mg on Al inhibition of root elongation was similar to that of soybean. Root elongation of cv Atlas 66 (Al-tolerant) was consistently superior to Scout 66 (Al-sensitive) when Al^{3+} was present at activities up to $5 \mu\text{M}$ in the basal solution with only $800 \mu\text{M}$ CaSO_4 (Figure 4). Similar differences in root elongation between the two genotypes have been reported previously (Pellet et al., 1996; Parker and Pedler, 1998). In contrast to the res-

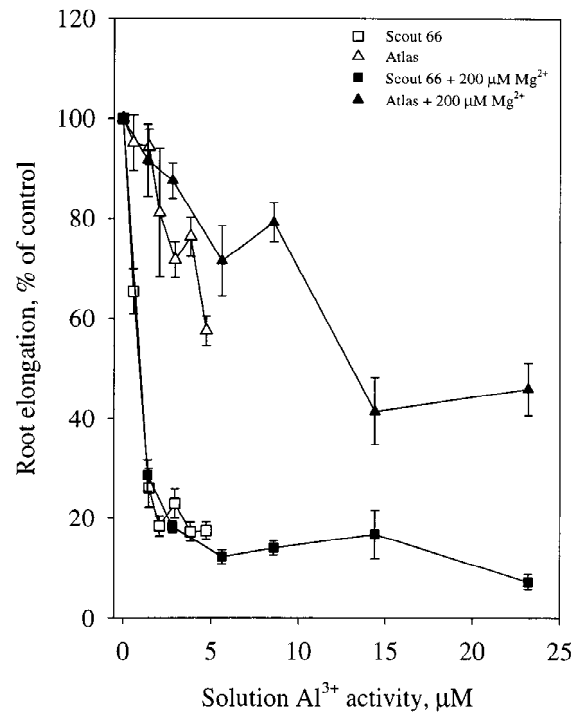


Figure 4. Relative root elongation of wheat genotypes Scout 66 and Atlas as a function of Al^{3+} activities in $800 \mu\text{M}$ CaSO_4 solutions and Mg supply. Bars denote standard errors.

ults with soybean, there was little difference in the root elongation response to Al^{3+} and genotypic differences in Al tolerance were not greatly modified when $200 \mu\text{M}$ Mg was added to the basal solution (Figure 4).

Calcium/Magnesium dose-response

The concentration dependence of the Mg effect was examined with soybean. When growing in the $800 \mu\text{M}$ CaSO_4 basal solution and $2.4 \mu\text{M}$ Al^{3+} activity, there was limited root elongation for cvs Essex and the PI when Mg was absent (Figure 5). With additions of Mg in the μM range, Al inhibition of root elongation was progressively alleviated for both genotypes. In the presence of $25 \mu\text{M}$ Mg , root elongation was enhanced by more than 50% and at $50 \mu\text{M}$ Mg root elongation exceeded that of the control treatments without Al. In contrast, additions of Ca in the same concentration range as for Mg had little impact on ameliorating Al rhizotoxicity.

Additional experiments were carried out to investigate the concentrations of Ca required to alleviate the inhibition of root elongation by Al. When only the basal solution was present ($800 \mu\text{M}$ CaSO_4), root elongation in the presence $2.4 \mu\text{M}$ Al^{3+} activity was

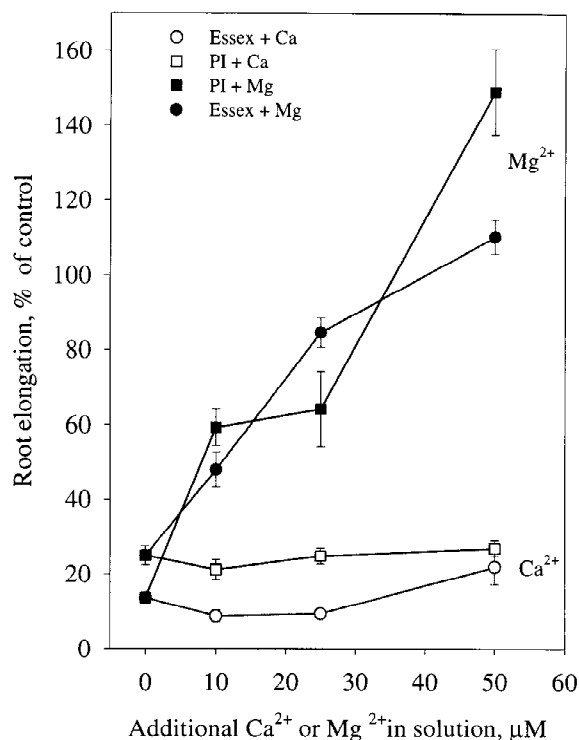


Figure 5. Effect of micromolar additions of Ca or Mg to 800 μM CaSO_4 solutions on relative tap root elongation of soybean genotypes Essex and PI in the presence of 2.4 μM Al^{3+} activity. Bars denote standard errors.

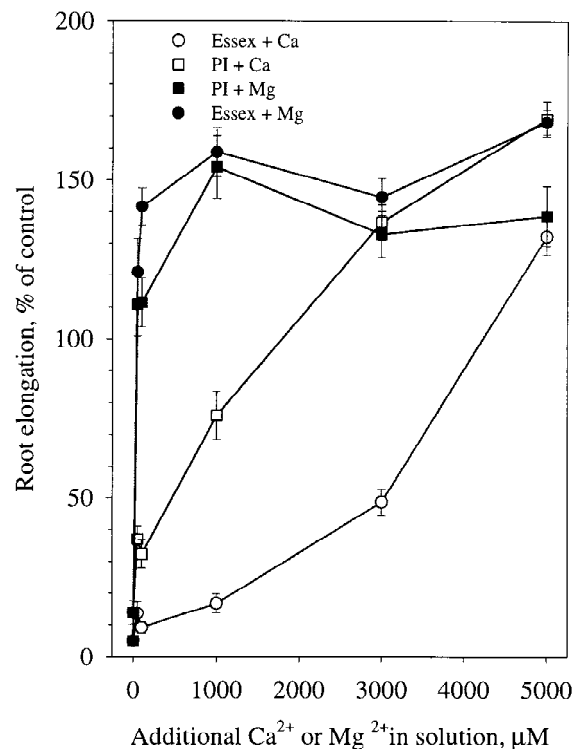


Figure 6. Effect of millimolar additions of Ca or Mg to 800 μM CaSO_4 solutions on relative tap root elongation of soybean genotypes Essex and PI in the presence of 2.4 μM Al^{3+} activity. Bars denote standard errors.

less than 20% of the control treatments without Al for both genotypes (Figure 6). As in other experiments, a low rate of Mg (50 μM) was able to completely alleviate Al rhizotoxicity in both genotypes (Figure 6). Root elongation in solutions with Al reached comparable values to the control solutions at Ca concentrations of 3000 μM for the PI and 5000 for cv Essex. The required Ca concentration exceeded that for Mg by over 60-fold.

Molar ratio replacement experiments between Mg and Ca were carried out to investigate the interactions between the cations on root elongation in the presence and absence of Al. In such experiments, confounding effects are minimized because solution ionic strength remains constant and changes in the plasma membrane electrical potential are avoided (Kinraide, 1998). Maximum root extension at a pH of 4.2 in the absence of Al was approached in the 100–400 μM Ca range (Figure 7). In the absence of Ca, even 600 μM Mg was ineffective in supporting root elongation. Roots were also exposed to solutions containing 9 μM Al^{3+} activity. Magnesium alone was ineffective in offsetting

Al inhibition of root elongation when Ca was absent. Additions of 600 μM Ca also failed to alleviate Al toxicity, whereas 200 μM Mg in combination with 400 μM Ca provided root elongation values that were about 80% of the maximum values obtained in solutions without Al. Increasing Mg from 300 to 500 μM , with a simultaneous reduction in Ca from 300 to 100 μM , reduced root elongation of plants exposed to Al. Since a similar reduction in root elongation did not occur when Al was absent from solutions, it is likely that the reduction in root extension at combination of high Mg and low Ca concentrations was related to an Al-induced Ca deficiency.

Discussion

The presence of Mg in nutrient solutions substantially decreased Al inhibition of root elongation in soybean. Amelioration occurred at μM concentrations of Mg with a number of soybean genotypes. The response to Mg appeared to be mechanistically different from Ca and the latter ion only became effective at mM

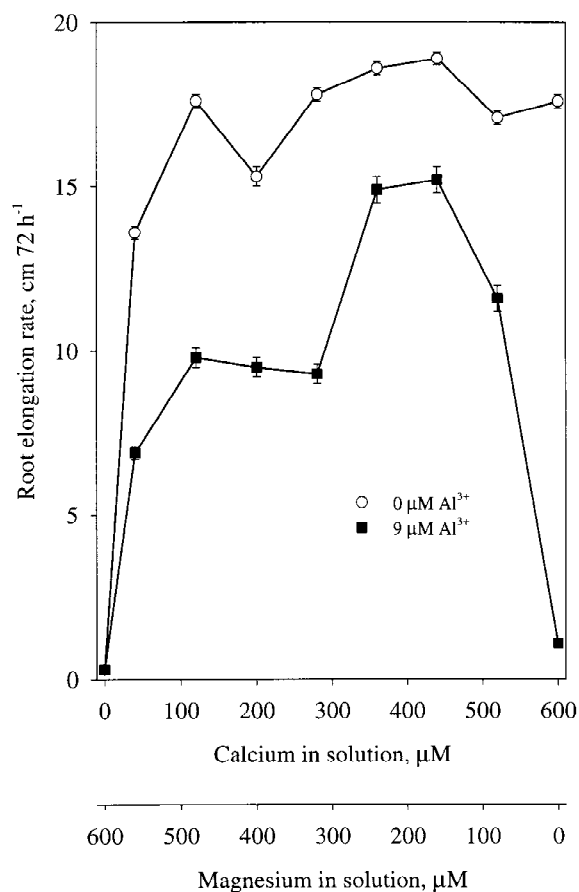


Figure 7. Tap root elongation rate of cultivar Essex in response to Ca and Mg concentrations in the absence and presence of $9 \mu\text{M}$ Al^{3+} activity. The total of Ca^{2+} and Mg^{2+} concentrations in solution was always maintained at $600 \mu\text{M}$. Bars denote standard errors.

concentrations. The change in soybean root response to Al by Mg also can be seen in the study by Lazof and Holland (1999), who compared Al effects on root extension in both CaSO_4 and complete nutrient solutions.

The short-term (72 h) experiments with wheat indicated that the presence of Mg did not substantially alter Al inhibition of root extension as with soybean. Results of other experiments on Mg and Al interactions with wheat, which also were short-term and used simple nutrient solutions, suggested that amelioration of Al toxicity appear to exist only when Mg was present in the mM range (Kinraide et al., 1985; Kinraide and Parker, 1987; Kinraide, 1994, Ryan et al., 1997). There also have been long-term experiments that examined Mg and Al interactions (Edmeades et al., 1991; Keltjens and Dijkstra, 1991; Keltjens and

Tan, 1993; Wheeler and Edmeades, 1995b). However, the need to maintain adequate Mg nutrition in control plants and the possibility of indirect Al effects on P and Ca nutrition make valid comparisons difficult.

Differences in Mg and Al interactions between soybean and wheat may be related to the differences reported by Keltjens and Tan (1993) among dicot and monocot species. Since their observations are based on dry matter yield and root length data for solutions with different Ca/Mg ratios was presented only as means across monocots and dicots, direct comparisons with our results are difficult. Recent results have demonstrated that there are differences in tolerance mechanisms for wheat and soybean. Exposure of wheat roots to Al triggers malate exudation (Delhaize and Ryan, 1995), whereas Al exposure in soybean triggers citrate accumulation at the root tip and excretion (Silva et al., 1999). Possibly, Mg has different effects on these two processes in wheat and soybean.

The mechanistic basis for the Mg amelioration of Al rhizotoxicity in soybean remains unclear. In the past, the ameliorative effects of cations at mM concentrations have been explained most convincingly in terms of changes in the electrical potential and Al^{3+} activity at root plasma membrane surface (Kinraide et al., 1992; Kinraide, 1994, 1998) or Al saturation at root cation exchange sites (Grauer and Horst, 1992). In our experiments, the ameliorative effect of Mg additions to solutions could not be attributed to increases in electrical potential and consequent reductions in Al^{3+} activity at the membrane surface because it occurred in the μM range. A positive response in root extension was detectable at $10 \mu\text{M}$ Mg and increased steadily up to $50 \mu\text{M}$ Mg. Under similar hydroponic conditions with $2.9 \mu\text{M}$ Al^{3+} activity in solution, additions of $50 \mu\text{M}$ Mg were estimated by a modified Gouy-Chapman-Stern model (Kinraide et al., 1998) to change the membrane electrical potential from -8.6 to -8.4 mV, and the Al^{3+} activity at the membrane surface changed from 7.9 to $7.8 \mu\text{M}$ (Silva, 2000). Calcium ions affect membrane negative potential in a manner similar to Mg ions (Kinraide et al., 1998), but additions of Ca to solutions in the μM range failed to alleviate the negative effects of Al on root elongation to the same extent as equal concentrations of Mg (Figure 5). There was, however, an absolute need for Ca in solution in order for the protective effect of Mg to be expressed (Figure 7).

The effectiveness of Mg on alleviating Al rhizotoxicity in the μM range suggests the involvement of biochemical/metabolic regulation. Previous experi-

ments using the Al-specific fluorescent stain lumogallion (Silva et al., 2000) have shown that genotypes more susceptible to Al rhizotoxicity accumulate more Al in meristematic cells at the root tip. This observation appears true with other plants species as well (Crawford et al., 1998; Delhaize and Ryan, 1995; Ryan et al., 1997; Samuels et al., 1997). The accumulation of Al causes a disruption of cell expansion and division (Kochian, 1995), which is primarily responsible for the associated decrease in root elongation. The presence of Mg may stimulate a series of events that would lead to more efficient detoxification of Al. This could occur by enhanced production of citric acid and other Al-chelating substances that either accumulate inside, are secreted out of the root tip or alleviate an Al competition with Mg at a sensitive binding site. Alternatively, Mg additions may correct an Al-induced Mg deficiency at the root tip. In yeast, Al blocks Mg uptake and reduces cell growth and this effect was suggested to be associated with an Al-induced Mg deficiency (MacDiarmid and Gardner, 1996). Accordingly, additions of Mg increased Mg uptake, restored cell growth, and overexpression of genes encoding Mg transporter proteins increased Mg uptake and conferred resistance to Al (MacDiarmid and Gardner, 1998). Aluminum inhibition of Mg uptake also has been suggested as a cause of Al toxicity in higher plants (Rengel and Robinson, 1989). Nonetheless, it does not seem that a Mg transport inhibition could be involved in our system as inhibition of root elongation occurred for plants exposed to Al when no Mg was present in solution.

Another important aspect of cation amelioration of Al toxicity is the magnitude of root growth response by a genotype. The Ca requirement to completely offset the negative effects of Al on root elongation was higher in susceptible genotypes (Figure 6). These results are in agreement with previous research in other plant species (Edmeades et al., 1991; Hecht-Buchholz and Shuster, 1987; Tan et al., 1992; Wheeler and Edmeades, 1995b) which indicated that higher cation levels in solution would be required by Al-susceptible genotypes in order to bring root elongation to that of solutions without Al. The greater production and secretion of citrate in the soybean root apoplast/rhizosphere of tolerant genotypes relative to sensitive ones (Silva et al., 1999) may be one of the main underlying causes of a differential Ca requirement in solution. Because of the strong alleviating effect on Al inhibition of root extension by μM concentrations of Mg, genotypic differences in relation

to Mg requirement were not evident. This indicates that the Mg protection against Al rhizotoxicity in soybean is offsetting the differential Al-susceptibility of the genotypes.

The ameliorative effect of Mg on inhibition of root elongation has implications to hydroponic procedures for screening for Al-tolerant soybean germplasm. Hydroponics is an important part of breeding programs searching for favorable genetic traits and rankings of soybean genotype sensitivity to Al in CaSO_4 solutions generally correspond with rankings in sand culture, although differences among genotypes are less in the latter (Horst and Klotz, 1990; Villagarcia et al., 2000). However, apparent Al tolerance with specific genotypes does not always result in better growth and yield in acid, Al toxic soils (Blamey et al., 1991; Horst and Klotz, 1990; Sartain and Kamprath, 1978). In experiments using soil, it is unclear whether the Mg/Al interaction alters tolerance, or whether there are other confounding factors.

Acknowledgements

This work was partially supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES)/Ministry of Education-Brazil through a scholarship to Ivo R. Silva (grant no. 2575/95-7).

References

- Alva A K, Edwards D G, Asher C J and Blamey F P C 1986 Effect of phosphorus/aluminum molar ratio and calcium concentration on plant response to aluminum toxicity. *Soil Sci. Soc. Am. J.* 50, 133–137.
- Barceló J, Poschenrieder C H, Vázquez M D and Gunsé B 1996 Aluminum phytotoxicity. A challenge for plant scientists. *Fert. Res.* 43, 217–223.
- Blamey F P C, Edmeades D C, Asher C J, Edwards D G and Wheeler D M 1991 Evaluation of solution culture techniques for studying aluminium toxicity in plants. *Dev. Plant Soil Sci.* 45, 905–912.
- Campbell G K A and Carter T E 1990 Aluminum tolerance in soybean: Genotypic correlation and repeatability of solution culture and greenhouse screening methods. *Crop Sci.* 30, 1049–1054.
- Carter T E and Rufty T W 1993 Soybean plant introductions exhibiting drought and aluminum tolerance. *In* *Adaptation of Food Crops to Temperature and Water Stress*. Ed. CG Kuo. pp 335–346. Asian Vegetable Research and Development Center, Publication No. 93-410, Taipei, Taiwan.
- Crawford S A, Marshall A T and Wilkens S 1998 Localisation of aluminum in root apex cells of two Australian perennial grasses by X-ray microanalysis. *Aust. J. Plant Physiol.* 25, 427–435.
- Delhaize E and Ryan P R 1995 Aluminum toxicity and tolerance in plants. *Plant Physiol.* 107, 315–321.

- Edmeades D C, Wheeler D M, Blamey F P C and Christie R A 1991 Calcium and magnesium amelioration of aluminum toxicity in Al-sensitive and Al-tolerant wheat. *In* Plant-Soil Interactions at Low pH. Eds. DC Wright, VC Baligar and RP Murrmann. pp 755–761. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Goldman I L, Carter T E and Paterson R P 1989 A detrimental interaction of subsoil aluminum and drought stress on the leaf water status of soybean. *Agron. J.* 81, 461–463.
- Grauer U E 1993 Modeling anion amelioration of aluminium phytotoxicity. *Plant Soil* 157, 319–331.
- Grauer U E and Horst W J 1992 Modeling cation amelioration of aluminium phytotoxicity. *Soil Sci. Soc. Am. J.* 56, 166–172.
- Hecht-Bushholz Ch and Shuster J 1987 Responses of Al-tolerant Dayton and Al-sensitive Kearney barley cultivars to calcium and magnesium during Al stress. *Plant Soil* 99, 47–61.
- Horst W J and Klotz F 1990 Screening soybean for aluminum tolerance and adaptation to acid soils. *In* Genetic Aspects of Plant Mineral Nutrition. Eds. N El Bassan, M Dambroth and BC Loughman. pp 355–360. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Howeler R H 1991 Identifying plants adaptable to low pH conditions. *In* Plant-Soil Interactions at Low pH. Eds. DC Wright, VC Baligar and RP Murrmann. pp 885–904. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Keltjens W G and Tan K 1993 The role of magnesium and calcium in alleviating aluminum toxicity in wheat plants. *In* Plant-Soil Interactions at Low pH. Eds. DC Wright, VC Baligar and RP Murrmann. pp 763–768. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Keltjens W G and Dijkstra W J 1991 Interactions between aluminium, magnesium and calcium with different monocotyledonous and dicotyledonous plant species. *Plant Soil* 155/156, 458–488.
- Kinraide T B 1991 Identity of the rhizotoxic aluminum species. *Plant Soil* 134, 167–178.
- Kinraide T B 1994 Use of a Gouy-Chapman-Stern model for membrane-surface electrical potential to interpret some features of mineral rhizotoxicity. *Plant Physiol.* 106, 1586–1592.
- Kinraide T B 1997 Reconsidering the rhizotoxicity of hydroxyl, sulphate, and fluoride complexes of aluminium. *J. Exp. Bot.* 48, 1115–1124.
- Kinraide T B 1998 Three mechanisms for the calcium alleviation of mineral toxicities. *Plant Physiol.* 118, 513–520.
- Kinraide T B and Parker D R 1987 Cation amelioration of aluminum toxicity in wheat. *Plant Physiol.* 83, 546–551.
- Kinraide T B, Arnold R C and Baligar V C 1985 A rapid assay to access aluminum phytotoxicity at submicromolar concentrations. *Physiol. Plant.* 65, 245–250.
- Kinraide T B, Ryan P R and Kochian L V 1992 Interactive effects of Al^{3+} , H^{+} , and other cations on root elongation considered in terms of cell-surface electrical potential. *Plant Physiol.* 99, 1461–1468.
- Kinraide T B, Yermiyahu U and Rytwo G 1998 Computation of surface electrical potentials of plant cell membranes. Correspondence to published zeta potentials from diverse plant sources. *Plant Physiol.* 118, 505–512.
- Kochian L V 1995 Cellular mechanisms of aluminum toxicity and resistance in plants. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* 46, 237–260.
- Lazof D B and Holland M J 1999 Evaluation of the aluminium-induced root growth inhibition in isolation from low pH effects in *Glycine max*, *Pisum sativum* and *Phaseolus vulgaris*. *Aust. J. Plant Physiol.* 26, 147–157.
- MacDiarmid C W and Gardner R C 1996 Al toxicity in yeast – a role for Mg? *Plant Physiol.* 112, 1101–1109.
- MacDiarmid C W and Gardner R C 1998 Overexpression of the *Sacharomices cerevisiae* magnesium transport system confers resistance to aluminum ion. *J. Biol. Chem.* 273, 1727–1732.
- Parker D R, Norwell W A and Chaney R L 1995 GEOCHEM-PC: A chemical speciation program for IBM and compatible personal computers. *In* Soil Chemical Equilibrium and Reaction Models. Ed. RH Loeppert. pp 253–270. SSSA Special Publication No 42. ASA/SSSA, Madison, WI.
- Rengel Z and Robinson D L 1989 Competitive Al^{3+} inhibition of net Mg^{2+} uptake by intact *Lolium multiflorum* roots. *Plant Physiol.* 91, 1407–1413.
- Ritchey K D, Silva J E and Sousa D M G 1983 Relação entre teor de cálcio no solo e desenvolvimento de raízes avaliado por um método biológico. *Braz. J. Soil Sci.* 7; 269–275.
- Ryan P R, Reid R J and Smith F A 1997 Direct evaluation of the Ca^{2+} -displacement hypothesis for Al toxicity. *Plant Physiol.* 113, 1351–1357.
- Samuels T D, Küçükakyüz K and Rincón-Zachary M 1997 Al partitioning patterns and root growth as related to Al sensitivity and Al tolerance in wheat. *Plant Physiol.* 113, 527–534.
- Sanchez P A and Salinas J G 1981 Low input technology for Oxisols and Ultisols in Tropical America. *Adv. Agron.* 34, 279–305.
- Sanzonowicz C, Smyth T J and Israel D W 1998 Calcium alleviation of hydrogen and aluminum inhibition of soybean root extension from limed soil into acid subsurface solutions. *J. Plant Nutr.* 21, 785–804.
- Sartain J B and Kamprath E J 1978 Aluminum tolerance in soybean cultivars based on root elongation in solution culture compared with growth in acid soil. *Agron. J.* 70, 17–20.
- Silva I R 2000 Aluminum rhizotoxicity in soybean: A physiological approach to cellular localization, tolerance mechanisms and alleviation by basic cations. Ph.D. Thesis, Soil Science Department, North Carolina State University, Raleigh, NC. 150 p.
- Silva I R, Smyth T J, Israel D W, Carter T E and Rufty T W 1999 Aluminum-induced changes in root content and exudation of organic acids are related to differential Al-tolerance among soybean genotypes. Abstracts of the 91st ASA Annual Meeting, Salt Lake City, UT. ASA/CSSA/SSSA, Madison, WI. 253 pp.
- Silva I R, Smyth T J, Moxley D F, Allen N S and Rufty T W 2000 Aluminum accumulation at nuclei of cells in the root tip. Fluorescence detection using lumogallion and confocal laser scanning microscopy. *Plant Physiol.* 123: 543–552.
- Spehar C R 1994 Aluminum tolerance of soya bean genotypes in short term experiments. *Euphytica* 76, 73–80.
- Tan K, Keltjens W G and Findenegg G R 1992 Aluminum toxicity with sorghum genotypes in nutrient solutions and its amelioration by magnesium. *J Plant Nutr.* Soil Sci. 155, 81–86.
- Villagarcia M R, Carter T E, Rufty T W, Arellano C, Niewoehner A S and Jennette M 2000 Screening for aluminum tolerance: A comparison of methodologies. *Crop Sci.* (in review)
- Wheeler D M and Edmeades D C 1995a Effect of ionic strength on wheat yield in the presence and absence of aluminum. *In* Plant-Soil Interactions at Low pH. Eds. RA Date, NJ Grundon, GE Rayment and ME Probert. pp 623–626. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Wheeler D M and Edmeades D C 1995b Effect of varying solution calcium or magnesium concentrations in the presence or absence of aluminum on yield and plant calcium or magnesium concentration in wheat. *J. Plant Nutr.* 18, 2229–2245.

Section editor: P. Ryan